Biomass of surface-foraging ants (Formicidae) in four bushland habitats in the wheatbelt of Western Australia

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Abstract

Using quadrat counts, biomass of surface-foraging ants was measured within four long unburnt bushland habitats in the Western Australian wheatbelt between January and November 1988. Bushland habitats were classified as mallee, woodland, shrubland and heath. Characteristics of plant litter, canopy and vertical density of vegetation to 3 m were determined for habitats. Prior to monthly ant counts, soil moisture and soil temperature were measured at 10 cm depths. Habitats differed significantly in biomass of surface-foraging ants. Mean dry ant biomass (+ S.E.) for mallee, woodland, shrubland and heath was 19.6 + 4.0, 6.9 + 1.1, 4.3 + 0.9 and 3.4 + 0.4 mg/m^2 respectively. Ants < 2 mm, 4 - 7 mm, and > 10 mm in length contributed little to biomass, irrespective of habitat. Ants 2 - 4 mm in length were most abundant in all habitats, accounting for 91 % of biomass in mallee. Ants 7 - 10 mm were also important in woodland, shrubland and heath. Biomass also varied temporally, with marked winter minima and summer maxima, and correlated with soil temperature in habitats other than heath. Soil moisture had no apparent effect on ant biomass, irrespective of habitat. The differences between the four habitats (with respect to plant litter, canopy and vertical density of vegetation) were assessed for the six possible pairs of habitats. Woodland and mallee were most similar, with 7/14 variables showing significant differences. Shrubland/woodland and shrubland/heath were most dissimilar, with 12/14 variables showing differences. Correlation analysis indicated that ant biomass was positively associated with woody litter, broad-leaf litter and vegetation density at 2.5 - 3 m height, and negatively with grassy litter, vegetation density at 0 - 0.5 m height, and the coefficients of variation of litter and canopy cover. These associations probably reflect the importance of these aspects of the habitats in providing ants with diversity of food and shelter, and suitable microhabitats and microclimates. The ant fauna in these reserves may reflect past disturbances or management strategies such as fire exclusion for at least 45 years, livestock grazing and selective logging for charcoal production.

Introduction

Ants are a conspicuous component of Australian ecosystems, being especially abundant and diverse in semi-arid environments where in excess of 150 species have been found within an area of only 0.5 ha (Andersen 1983, 1984). Given their abundance and diversity, ants fulfil a major role in ecosystems through soil aeration and drainage, nutrient and seed redistribution, plant pollination, and general predator-prey interactions (Buckley 1982, Abensperg-Traun 1988, Lobry de Bruyn & Conacher 1990).

Australian studies on ant ecology have examined their diversity (Andersen 1983, 1986), periodicity in patterns of activity (Briese & Macauley 1980, Andersen 1983), community structure (Briese & Macauley 1977, Morton & Davidson 1988), interactions with physical soil parameters such as structure and particle size distributions (Greenslade & Thompson 1981, Lobry de Bruyn 1990), their role in seed dispersal (Berg 1975, Drake 1981), short-term effects of fire on ant community parameters (O'Dowd & Gill 1984, Andersen & Yen 1985), and their usefulness as bioindicators (Majer 1983, Andersen 1990). Alternatively, they have focused on prominent species such as the meat ant *Iridomyrmex purpureus* (Greaves & Hughes 1974, Greenslade 1975, 1976) and bull ants, *Myrmecia* spp. (Gray 1971). Characteristics of vegetation, such as structural complexity, and plant litter, are known to influence ant populations in Australia (Greenslade and Thompson 1981, Andersen 1986). Few studies, however, have quantified the relationship between ant abundance and vegetation and plant litter parameters (e.g. Majer *et al.* 1984). Sound knowledge of the conditions best suited for a thriving ant fauna is essential for the successful rehabilitation of degraded environments (Majer *et al.* 1984).

The Western Australian wheatbelt has experienced extensive land-clearing for agriculture between 1900 and 1970. Today, native vegetation remnants of the region are generally small, isolated to varying degrees and often degraded through livestock grazing and weed invasion. In addition, this study area has been unaffected by fire for at least 45 years, and this may have had a significant influence on its ant fauna (see O'Dowd & Gill 1984, Andersen & Yen 1985). Although an absence of fire since about 1945 is not unusual in the wheatbelt, other regions of Western Australia, such as the extreme southwest, have had more frequent fires. In recognition of the need to understand the ecological dynamics of these remnants, long-term research into its faunal and floral components is being conducted (Main 1987, Saunders *et al.* 1987). The present study forms a part of this research activity and was carried out as part of a larger study into the foraging ecology of the echidna (Abensperg-Traun 1990). It describes the results of an 11-month ant survey of four long unburnt habitats in two Western Australian wheatbelt reserves, and it emphazises surface-foraging ant species because these make up the bulk of ants in southern Australia (Greenslade 1979). The study has three aims: (i) to determine differences in biomass of surface-foraging ants in relation to habitat; (ii) to examine soil moisture and temperature as determinants of surface-activity; and (iii) to determine any associations that exist between vegetation and plant litter and biomass of surface-foraging ants.

Materials and Methods

Study area

The study was conducted in Durokoppin East Nature Reserve (31°24'S, 117°45'E; 1030 ha) and Kodj Kodjin Nature Reserve (31°27'S, 117°47'E; 204 ha) of the Western Australian wheatbelt, between January and November 1988. The Reserves lie <400 m above sea level with an altitudinal relief of <75 m. They are connected by a continuous strip of native vegetation 2.7 km long and 40 m wide. The region is semi-arid (Gentilli 1965), with a mean annual precipitation of 334 mm, which falls mostly in the winter months from May to August (Beard 1980). Ambient temperature and rainfall data for Kellerberrin are given in Table 1.

Table 1

Mean monthly rainfall (mm) and minimum and maximum monthly ambient temperatures (°C) for Kellerberrin (Beard 1980).

	J	F	M	A	M	J	J	A	S	O	N	D
Rainfall (mm)	10	15	22	22	43	57	53	42	26	18	11	13
Min. temp. (°C)	16	20	16	11	7	8	7	7	7	9	14	14
Max. temp. (°C)	34	34	32	25	22	20	17	17	22	24	29	29

The vegetation in these two reserves has been unburnt for at least 45 years. I grouped the vegetation into structural units (Beadle & Costin 1952) because we know these to be important influences on the abundance and distribution of the Australian ant fauna (Greenslade & Thompson 1981). Groups that I recognized were open woodland, mallee, shrubland and heath. Woodland, mallee and heath are fully described in Abensperg-Traun and De Boer (1990). Shrubland is dominated by *Allocasuarina campestris*, with some *Leptospermum* and *Melaleuca* species. It is dense (90-100% projected canopy cover), and grows to about 3 m in height. Ground cover is moderately extensive (40-50%) and consists of fallen debris from shrubby plants (mostly *Allocasuarina* needles), with some grasses and herbs. Surface lateritic gravel overlies sandy subsoils in most areas. The distribution and area of each habitat within the Reserves is given in Fig 1 and Table 2.

Table 2

Habitat contributions to reserve area

Habitats	Durokoppin Reserve		Kodj Kodjin Reserve	
	Area (ha)	% of reserve	Area (ha)	% of reserve
Woodland	321	31	112	55
Mallee	44	4	56	28
Shrubland	351	34	31	15
Heath	323	31	4	2
Other[1]	1	<1	1	<1

[1]rocky outcrops; gravel and sand pits.

For sampling purposes, I considered the two reserves as representing a single area of native vegetation because of their close proximity and connectivity to each other, because of the similarity of their soils, flora and fauna, and their similar fire history (Dell 1978, Muir 1978, Chapman & Kitchener 1978, Dell & Chapman 1978, W.M. McArthur, unpubl. manuscript). I distributed study plots unevenly between the reserves (Fig 1) because of difficulties to gain access to suitable patches of mallee in Durokoppin, and heath and shrubland in Kodj Kodjin.

Ant sampling

Pitfall traps are an accepted method to measure the activity of surface foraging ant species. Such traps integrate the whole 24-hour cycle of activity, as well as day-to-day variation, and are frequently used to assess Australian ant faunas (Greenslade 1973, Rossbach & Majer 1983). Yet during a previous study where pitfall traps were used (Abensperg-Traun 1988), a source of bias was identified. Here, individuals of a particularly abundant, small species of *Iridomyrmex* appeared to follow colony members into trapping pits, thus leading to potential overestimation of densities. For the present study, I therefore chose a visual sampling technique to measure spatial and temporal variations in biomass of surface-foraging species (Briese & Macauley 1980).

Ant densities in habitats were determined by counting ants in 10 randomly positioned 1 m² quadrats. These counts were carried out in each of six 2500 m² study plots for each habitat. Quadrat positions changed monthly. Shrubland was not sampled in January and February, and only two study plots were allocated to shrubland (see Table 3). Plots were sampled monthly, in random order, and at a time of day when ants were known from observation to be active, ie. early mornings during summer (at sunrise), and afternoons in winter (no sampling was done during rain). Given that relative, not absolute, abundances were measured, the fact that only a proportion of colony members are likely to have been active at any one time (Chew 1960) is not critical. To avoid pseudoreplication, plots were chosen such that they were in interspersed
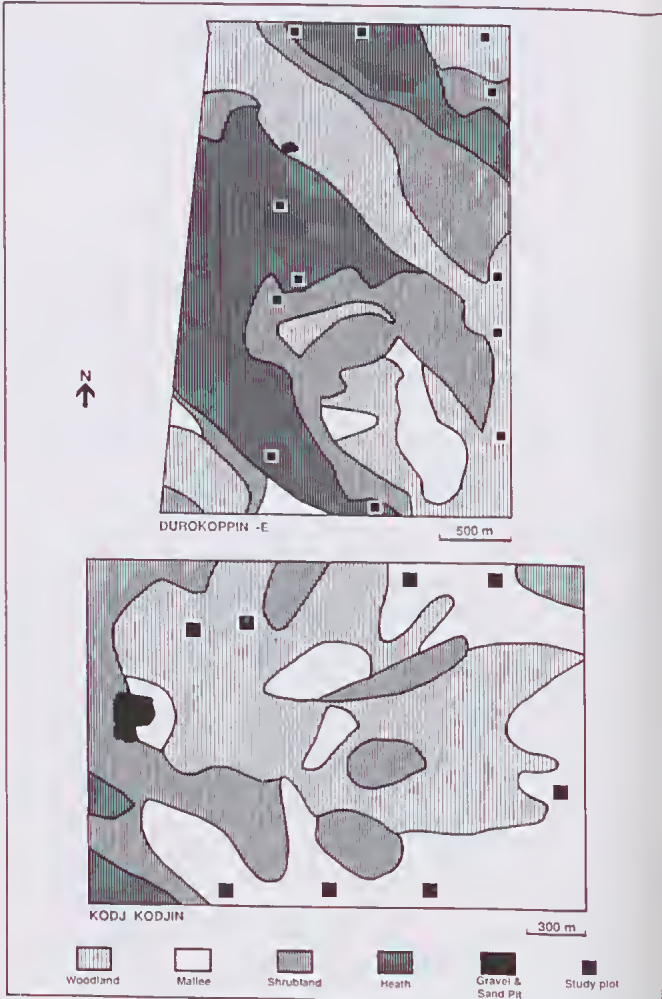

Figure 1. The distribution of study plots within the major vegetation types in Durokoppin and Kodj Kodjin Nature Reserves, Western Australia.

patches of the different habitats (Hurlbert 1984; Fig 1); the total area within which study plots were placed is given in Table 2. Surface foraging ants were counted and placed into five size categories: < 2 mm, 2 - 4 mm, 4 - 7 mm, 7 - 10 mm, and > 10 mm. Counts per quadrat lasted two minutes (see Anderson 1991). Dry mass was estimated from a linear regression between length and dry weight of ten local ant species representing the range of sizes and major castes, if dimorphic castes ($y = 0.366x + 0.024$; $r_o = +0.94$, P < 0.0001; from Abensperg-Traun 1990).

The use of a quadrat method to measure ant activity and the restriction of sampling to daytime periods may have introduced two potential sources of bias: (i) the differential sampling of diurnal vs. nocturnal species (see Briese & Macauley 1980, Andersen 1983). While strictly nocturnal species probably were not sampled, most surface-foraging species were accounted for because I sampled very early mornings in summer and afternoons in winter when ants are believed to be most active in southern Australia (Andersen 1983). By comparing habitats based on ant biomass on the surface (at sampling time), I assume that the contribution of nocturnal species to surface biomass is similar for the range of habitats that I measured. This is a reasonable assumption because opportunistic examinations at night suggested that the activity of the most abundant species (*Iridomyrmex*) extended well into the sampling period, and only a small number of species provide the bulk of ants in the study area. In fact, numerically, Abensperg-Traun (1988) found a single, small species of *Iridomyrmex* to account for the majority of ants sampled in all the habitats. Nevertheless, biomass values may be underestimates; and (ii) the potential over-sampling of large vs. small ants. Counting ants in quadrats may result in a bias in favour of larger ants because small ants are difficult to see, especially in areas of abundant litter. I took great care to locate such specimens by turning over plant litter.

Soil variables

In southern Australia, soil temperature and soil moisture are the predominant influences on the foraging activity of ants (Andersen 1986). My observations suggested that the nests of the numerically dominant *Iridomyrmex* lie close to the soil surface, hence I measured these two parameters at 10 cm depth in all the habitats except shrubland, taking one measure from each study plot and for every month. Soil temperature was determined by using copper-constantan welded tip P.T.F.E. insulated (type K) thermocouples (Taylor & Jackson 1965, Haverty *et al*. 1975). The soldered temperature-sensitive junctions were buried at 10 cm depth for the duration of the study. The positive and negative ends were plugged and protectively stored in a buried styrofoam container just below the soil surface which allowed instant temperature readings to be taken through a digital hand-held temperature indicator, and without disturbing ant activity. Details of soil moisture measurement were given in Abensperg-Traun and De Boer (1990). Both soil moisture and temperature were deter-mined five minutes prior to ant counts.

Table 3
Experimental design and ant sampling regime.

Habitats Sampled for ants	Number of study plots		No. of months sampled	No. of monthly ant quadrats per plot	Tot. no. of ant quadrats per plot
	Durokoppin Reserve	Kodji Kodjin Reserve			
Woodland	4	2	11	10	660
Mallee	0	6	11	10	660
Shrubland	2	0	9	10	180
Heath	6	0	11	10	660

Vegetation variables

I measured 14 variables at 36 predetermined sampling stations in each study plot (at regular 10 m intervals) once: (i) the percentage of soil surface covered by plant litter in a 1 m^2 quadrat, LITT; (ii) the coefficient of variation of litter cover, CVLITTCOV, calculated from "(i)"; (iii) the amount of woody litter, calculated as a percentage of "(i)" (twigs, branches, logs, *Eucalyptus* nuts, bark), WOODYLITT; (iv) the amount of broad-leaf litter, calculated as a percentage of "(i)" (*Eucalyptus* spp.), BROADLITT; (v) the amount of narrow-leaf litter, calculated as a percentage of "(i)" (*Allocasuarina* spp. and assorted shrubs), NARRLITT; (vi) the amount of grassy litter, calculated as a percentage of "(i)" (including herbs and sedge, such as *Ecdeiocolea monostachya*), GRASSLITT; (vii) the percentage of pro-jected canopy cover, measured from ground level using a spherical densiometer as in Lemmon (1956), CANCOV; (viii) the coefficient of variation of canopy cover, CVCAN-COV, calculated from "(vii)"; (ix) the vertical density of vegetation at a height of 0 - 0.5 m, VEG 0 - 0.5 m; (x) at 0.5 - 1 m, VEG 0.5 - 1 m; (xi) at 1-1.5 m, VEG 1 - 1.5 m; (xii) at 1.5 - 2 m, VEG 1.5 - 2 m; (xiii) at 2 - 2.5 m, VEG 2 - 2.5 m; and (xiv) at 2.5 - 3 m, VEG 2.5 - 3 m. Vegetation density was measured with a canopy intercept method where a rod is passed vertically through the vegetation and the number of vegetation intercepts within the specified strata are counted. An increase in the number of intercepts is interpreted as an increase in vegetation density (Frank and McNaughton 1990).

Analysis

The following transformations were made to improve linearity of the data: mean ant biomass (log); vegetation density (square root); percentage litter cover, litter type and canopy cover (arcsine) (Underwood 1981). To deter-mine the effects of habitats and time on ant biomass, I analysed means of quadrats of ant biomass within the plots (dry weight mg/m^2) by non-orthogonal split-plot ANOVA (Steel & Torrie 1981). Using the the mean values for study sites, I applied simple linear regressions to correlate ant biomass with soil, litter and vegetation variables. Habitat differences in plot means of plant litter and vegetation values were analysed by Tuckey's Paired Comparison Procedure (Tuckey 1953). Computations were carried out using GENSTAT 5 Release 1.3 (Sun/Unix) (Payne *et al*. 1988).

Results

Ant biomass and soil variables

Ant biomass generally followed an annual cycle, with peaks and troughs at hottest and coldest times of the year, respectively. These fluctuations were most pronounced in mallee and least pronounced in heath (Fig 2). Surface ant biomass was independent of soil moisture at 10 cm depth, regardless of habitat, but was significantly correlated with soil temperature at 10 cm depth in woodland (r = +0.87, d.f. = 10, P < 0.001) and mallee habitats (r = +0.92, d.f. = 10, P < 0.001). In heath, biomass remained relatively constant throughout the year, suggesting that ants may have foraged evenly between seasons. Soil temperature at 10 cm depth was thus not a good predictor of ant activity in heath. Woodland, mallee and shrubland biomass declined sharply when soil temperature near the surface fell below about 17° C. Monthly soil temperature and soil moisture did not vary significantly between the habitats (P > 0.05).

Ant biomass and vegetation variables

There was a highly significant effect of habitat on ant biomass (Table 4). This strong habitat effect was estimated from the between-habitat variance of ant biomass of 35.7689 on 3 degrees of freedom, as against a within-habitat

estimate of variance of 3.1995 on 11 degrees of freedom. Orthogonal comparisons indicate that most of this strong habitat effect was accounted for by differences between mallee and the remaining habitats (F = 27.64, d.f. = 1/11, P < 0.001). There was a significant effect of time (month) on biomass, and a significant habitat x time (month) interaction (Table 4). The interaction was probably due to the large increase in ant biomass in the mallee habitat from November to March, which exceeded the increase in all other habitats (Fig 2).

The mean number of ants/m^2 ($\pm$ S.E.) in each habitat was 18.0 $\pm$ 3.6 (mallee), 5.2 $\pm$ 1.0 (woodland), 2.7 $\pm$ 0.8 (shrubland) and 2.0 $\pm$ 0.3 (heath) (Table 5). Mallee had the highest biomass in all months except July, when ant activity was lowest and habitats were most similar. Mean ant biomass (dry mg/m^2) in each habitat was 19.6 $\pm$ 4.0 (mallee), 6.9 $\pm$ 1.1 (woodland), 4.3 $\pm$ 0.9 (shrubland) and 3.4 $\pm$ 0.4 (heath). The ant size categories of 2 - 4 and 7 - 10 mm were most abundant in woodland, heath and shrubland habitats, while in mallee only ants of 2 - 4 mm length were abundant, accounting for 91% of biomass (Table 6). Most specimens in the 2 - 4 mm category were attributed to a single species of *Iridomyrmex*. Ant size categories other than those between 2 - 4 and 7 - 10 mm contributed little to total biomass in all habitats.

Characteristics of litter and vegetation are given in Tables 7 and 8 and Fig 3. Woodland and mallee were most similar, with 7/14 variables showing significant differences. Shrubland/woodland and shrubland/heath were most dissimilar, with 12/14 variables showing differences.

Ant biomass (averaged across all monthly samples) was positively correlated with woody litter, broad-leaf litter and vegetation density at 2.5 - 3 m, and negatively with grassy litter, vegetation density at 0 - 0.5 m and the coefficients of litter cover and canopy cover, but not with other variables (Fig 4). However, r^2 values were low, accounting for < 54 % of the variation in ant biomass.
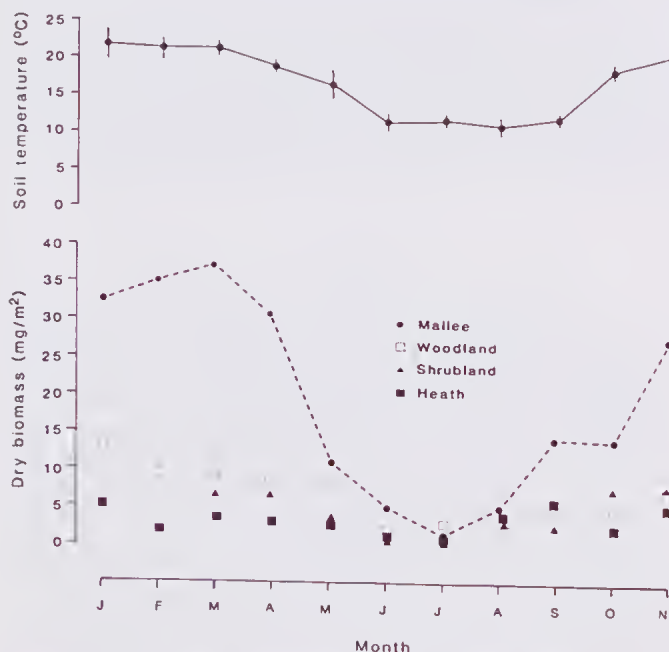
Discussion

Ant biomass and soil variables

Observed activity patterns showing summer maxima and winter minima are characteristic of ant faunas subjected to marked seasonal climatic regimes (Majer 1980, Greenslade & Greenslade 1984). While foraging activities in ants may also be influenced by biotic factors such as the presence and condition of larvae in nests, food availability and amounts of food stored (Weber 1972, Whitford & Ettershank 1975), surface activity in this study was strongly

Table 4

Summary table of non-orthogonal analysis of variance (via regression) of dry ant biomass (mg/m^2).

Source of variance	d.f.	s.s.	m.s.	F	P
Study plots	5	7.8025	1.5605	<1	n.s.
Habitats	3	107.3067	35.7689	11.18	**
Error	11	35.1946	3.1995		
Months	10	108.2027	10.8203	13.37	***
Habitats x months	28	36.3691	1.2989	1.60	*
Error	158	127.8900	0.8094		
Total	215	422.7656	1.9664		

* 0.01 < P < 0.05
** 0.001 < P < 0.01
*** P < 0.001
n.s. not significant

Table 5

Mean number of ants per m^2 ($\pm$ S.E.) for each month in woodland, mallee, shrubland and heath habitats.

Month	Habitat			
	Woodland (n[1] = 60)	Mallee (n = 60)	Shrubland (n = 20)	Heath (n = 60)
January	12.1±1.7	30.0±1.3	N.S.[2]	4.3±0.9
February	8.2±1.8	31.3±2.0	N.S.	1.9±0.2
March	7.4±1.3	34.0±0.9	3.3±0.4	1.3±0.2
April	6.4±0.9	26.7±1.1	5.2±0.3	1.9±0.1
May	6.1±0.9	10.4±0.9	1.8±0.1	1.7±0.2
June	1.5±0.3	4.3±0.7	0.5±0.1	1.0±0.2
July	1.8±0.2	1.9±0.1	0.3±0.1	0.5±0.2
August	1.8±0.4	4.4±0.8	0.2±0.1	1.3±0.2
September	3.3±0.2	15.3±0.5	1.6±0.3	2.5±0.5
October	2.8±0.3	12.7±0.8	5.7±0.1	1.5±0.1
November	5.7±0.9	27.5±1.0	5.8±1.6	3.7±0.6
December	N.S.			
Mean (all months)	5.2±1.0	18.0±3.6	2.7±0.8	2.0±0.3

[1]n = monthly number of sample quadrats. [2]N.S. = Not sampled.

Table 6

The percentage contribution of ant size categories (measured in mm) to total dry biomass on the soil surface for woodland, mallee, shrubland and heath habitats (mean ± S.E.).

Habitat	% Contribution of Ant Size Categories				
	<2	2-4	4-7	7-10	>10
Woodland	7.8±2.6	45.6±3.9	1.4±0.5	44.4±4.7	0.8±0.5
Mallee	5.1±1.5	91.2±1.7	0.1±0.1	3.5±1.4	0.1±0.1
Shrubland	1.1±0.7	56.9±6.7	0.0	41.6±6.4	0.4±0.2
Heath	1.0±1.3	40.9±3.3	1.2±0.6	55.7±3.3	1.2±0.6

Figure 2. The relationship between soil temperature (°C) at 10 cm depth (mean across all habitats, + S.E.), and monthly fluctuations of dry ant biomass (mg/m^2) on the soil surface for woodland, mallee, shrubland and heath habitats. Average standard errors of the mean ant biomass: woodland 3.6, mallee 13.3, shrubland 2.8, heath 1.5 mg/m^2. Mallee data points have been joined so as to highlight the observed differences in ant biomass between mallee and the other habitats.

associated with soil temperature in woodland and mallee faunas, though not in heath. The observed lack of an association between foraging activity in heath and soil temperature may have been due to insufficient foraging data (ie. low numbers of ants) rather than differences in ant tolerance to soil temperature extremes. While soil moisture apparently did not directly affect biomass, humidity did influence ant activity as evidenced by incidental observations showing increases in nest excavations when levels of humidity were high, such as shortly before and after rain.

Ant biomass and vegetation variables

Characteristics of vegetation influence ant communities through their effects on microclimate, carrying capacity (food sources and quantities) and structural complexity of the habitat (Greenslade & Greenslade 1977). Biomass of surface-foraging ants was high where woody litter, broad-leaf litter and vegetation density at 2.5 - 3 m were also high. These variables probably represent factors which contribute to habitat complexity which, elsewhere, are known determinants of the abundance of ants (Greenslade & Thompson 1981, Greenslade & Halliday 1983). Woody and broad-leaf litter provide nesting and foraging sites, microhabitats, food supplies and shelter from ambient temperature extremes (Greenslade & Greenslade 1977), while small trees (2.5 - 3 m) might provide food such as seeds, insects and sap (Andersen 1983), and protection from heat and direct sunlight, and possibly also higher relative humidity due to shade.

Biomass was low where grassy litter, vegetation density at 0 - 0.5 m, and the coefficients of variation of litter and canopy cover were high. Ants thus favoured areas of evenly distributed litter and canopy. The importance of an even canopy cover might reflect the need for suitable microclimatic conditions (shade) for foraging, which is probably of particular significance in the Western Australian wheatbelt where summer air temperatures reach 45°C in the shade. I have observed that dense vegetation at ground level is often associated with lack of bare patches of soil, and such areas are often avoided by foraging ants (Andersen 1983). Greenslade and Thompson (1981) also found certain species to be absent under dense vegetation, which they attributed to the relatively low temperatures experienced under such conditions. High values of grassy litter were generally associated with *Ecdeiocolea monostachya* (sedge) in heath, which was not favoured by ants. Sedge litter appears comparatively unsuitable for providing ants with diversity of microhabitat and adequate sources of food.
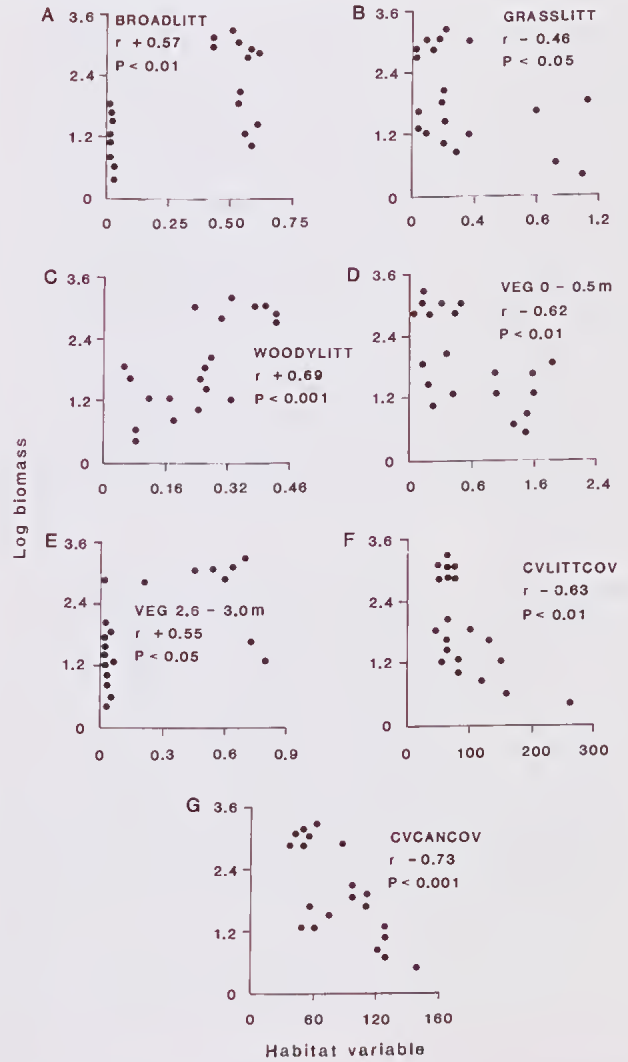

Figure 4. Correlations between log ant biomass (average of all months) and seven plant litter and vegetation variables for twenty study plots in four vegetation structural units (df = 18). Only those variables with significant correlations are listed. A broad-leaf litter (BROADLITT); B grassy litter (GRASSLITT); C woody litter (WOODYLITT); D vegetation density at 0 - 0.5 m height (VEG 0 -0.5 m); E vegetation density at 2.5 - 3.0 m height (VEG 2.5 - 3.0 m); F coefficient of variation of litter cover (CVLITTCOV); G coefficient of variation of canopy cover (CVCANCOV).

Figure 3. Vertical vegetation density [(number of intercepts)^0.5] between 0 and 3 m for the four habitats.

Greenslade (1979, p 3) stated that (in the South Australian environment) "the ideal situation for ants consists of a mosaic of bare soil and areas of herbs, small shrubs and grasses, under an open canopy of trees or taller shrubs". Andersen (1983) considers mallee vegetation to closely resemble Greenslade's (1979) ideal habitat for ants. In the Western Australian wheatbelt, mallee is apparently also the most suitable habitat for ants because biomass was highest there. Despite the similarity of woodland and mallee habitats in many of the habitat parameters measured (Table 8), there are potential explanations for the enormous biomass difference between these two habitats. Mallee is characterized by relatively large areas of bare ground, interspersed with areas of abundant litter, and these are often favoured for unimpeded foraging and nest excavation in ants (Andersen 1983). Further, more abundant broad-leaf litter and a higher vegetation density at 2 -3 m height in mallee may provide more abundant and diverse sources of food and a favourable microhabitat and microclimate.

Ant biomass for woodland was significantly higher than that for heath (t = 2.91, d.f. = 65, P < 0.005). In an eastern Australian study, Andersen (1986) also found ants to be more abundant in woodland, and he attributed this difference to woodlands' greater structural complexity; one would expect ant faunas at Kellerberrin to be similarly affected. Low ant biomass in heath may be due to the lack of intermediate-sized shrubs and trees, low diversity of plant litter and soils that are very sandy (and thus possibly not sufficiently stable for subterranean nest and gallery construction for some ant species). Shrubland had low ant biomass, possibly because canopy frequently approached 100% cover and afforded little light at ground level, thus adversely affecting microclimatic conditions (Carlson &

Gentry 1973, Greenslade & Thompson 1981). The diversity of litter as a source of food was low, with only a small woody and broad-leaf component. Shrubland is relatively poor in seed production (Van Schagen 1986), and seeds may form important dietary items for harvesting species such as *Pheidole* and *Monomorium* (Briese 1974); termite abundance in shrubland is also comparatively low (Abensperg-Traun & De Boer 1990), and I have observed termites to be important food for predatory *Iridomyrmex* (also reported in Greenslade 1970).

The observed weak associations ($r^2 < 54\%$) between ant biomass and vegetation and litter characteristics may have been influenced by a range of factors inherent in the study design. For instance, only extremes of habitat were sampled, thus a few points in one particular habitat may have had a strong influence on the strength of the association (e.g. see Fig 4A). Further effects may derive from the use of 11-month averages for ant biomass data, the measurement of physical habitat characteristics (vegetation structure and plant litter) at only one time and in different quadrats to the biomass measurements, and the uneven distribution of study plots between the two reserves. However, given the similarity of soil, vegetation and fire history of these closely adjacent reserves, it is unlikely that their ant faunas differ significantly in abundance and composition.

The Nature Reserves at Kellerberrin have experienced a range of disturbance regimes in the past. Woodland and mallee, in particular, were subjected to selective logging for charcoal production (between 1940 and 1945) as well as periodic livestock grazing, thereby reducing its naturally sparse understorey and possibly also affecting soil structure through hoof-pressure (King & Hutchinson 1976). Intermittent livestock grazing continues along the reserve margins during sheep mustering. Such disturbance re-

Table 7

Habitat characteristics of plant litter and canopy (mean ± S.E.).

Habitat	n[1]	Litter Cover (%)	Litter type (%)				Canopy Cover (%)	CV[2] Litter Cover	CV Canopy Cover
			Woody	Broad-leaf	Narrow-leaf	Grasses + herbs			
Woodland	216	51±3	46±2	37±2	6±1	11±2	34±3	59±5	71±11
Mallee	216	35±5	36±2	53±4	3±1	8±3	39±1	62±5	51±3
Heath	216	9±1	10±6	1±1	24±21	65±27	14±1	155±23	124±8
Shrubland	72	46±2	14±2	2±1	79±3	5±1	91±4	71±4	50±1

[1]n = sample size
[2]CV = coefficients of variation

Table 8

Summary table of Studentized Range Values[1] of comparisons between pairs of habitats for plant litter and vegetation parameters, using Tuckey's Paired Comparison Procedure (Tuckey 1953).

Variables	W v M[2]	W v H	W v S	M v H	M v S	H v S
% Litter cover	12.81**	58.16**	7.72**	35.97**	10.23**	35.67**
Litter variability (CV)	0.251	7.27**	0.59	4.05*	0.41	35.67**
% Canopy cover	1.28	6.98**	11.66**	6.21**	18.38**	6.44**
Canopy variability (CV)	5.41**	5.33**	3.86*	10.74**	0.04	27.17**
% Woody litter	3.60*	4.83*	3.76*	6.03**	7.36**	6.24**
% Broad-leaf litter	3.53*	32.37**	18.84**	28.85**	20.58**	2.18
% Narrow-leaf litter	0.10	3.03*	8.48**	3.10	14.79**	0.18
% Grassy litter	0.27	6.10**	1.02	7.27**	0.83	10.40**
Veg. density 0-0.5 m	0.47	19.07**	8.89**	11.39**	6.76**	4.87*
Veg. density 0.5-1 m	1.10	1.21	11.78**	1.99	21.50**	10.18**
Veg. density 1-1.5 m	0.04	0.23	33.75**	0.25	58.49**	18.69**
Veg. density 1.5-2 m	3.76*	1.18	56.99**	3.65*	93.39**	58.13**
Veg. drensity 2-2.5 m	5.32**	0.49	62.69**	6.83**	101.06**	97.04**
Veg. density 2.5-3 m	5.84**	—	8.83**	8.26**	7.04**	107.90** 15.29**

[1]Levels of significance are indicated by * 0.01 < P < 0.05, ** P <0.01; — insufficient data.
[2]W = woodland, M = mallee, H = heath, S = shrubland.

gimes might favour ant species that thrive in disturbed environments (e.g. *Iridomyrmex*). The overwhelming numerical dominance and surface biomass of a single species of *Iridomyrmex* (c. 3 mm) in mallee, and to a lesser extent in woodland (see also Abensperg-Traun 1988), might be indicative of an opportunistic species exploiting a disturbed environment. This study provides no data on numbers of species for habitats. Yet, recalling the 71 species recorded from two 50 m x 25 m plots in semi-arid mallee of north-western Victoria (Andersen 1983), observations in this study suggest that the mallee ant fauna at Kellerberrin was of comparatively low species diversity.

It needs to be understood that the habitats that I measured have been unaffected by fire for at least 45 years. Yet fire is an important factor in the regeneration of *Eucalyptus* spp. through seed fall and the activities of harvester ants (Ashton 1979, O'Dowd & Gill 1984). Also, fire is known to increase seed-predator satiation (Wellington & Noble 1985, Andersen 1988), thus increasing the success of seedling establishment (Andersen and Yen 1985). I observed a general absence of young eucalypts in woodland and mallee, and this may well be a consequence of an altered fire regime (R Hobbs, personal communication).

Similarly, ant faunas may benefit by periodic fire through a release from competition with increasingly dominant species, such as *Iridomyrmex* (Greenslade 1976, Whelan 1980, O'Dowd & Gill 1984, Andersen & Yen 1985). The overwhelming numerical dominance of a single species of *Iridomyrmex* in mallee and woodland habitats may well be sustained and exacerbated by the prolonged exclusion of fire as a factor of disturbance. The associated consequences to the maintenance of ecological processes, such as seedling survival through seed dispersal by ants, are poorly understood. Given the long duration of fire exclusion in Durokoppin and Kodj Kodjin Nature Reserves, the present study could be used as the basis for experimental studies into fire-ant-habitat interactions.

In summary, of the four habitats that I measured, biomass of surface-foraging ants was overwhelmingly superior in mallee, possibly because the combination of abundant woody- and broad-leaf litter, and high vegetation density at a height of 2.5 - 3 m, provided ants with diverse and abundant food and shelter, microhabitats and suitable microclimates. In the Western Australian wheatbelt, mallee may therefore most closely resemble Greenslade's "ideal" habitat for ants. However, the bushland reserves that formed the basis of this study have been unaffected by fire for at least 45 years. This, combined with past disturbances such as logging and grazing, may have influenced the relative suitability of woodland, mallee, shrubland and heath for foraging ants.

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